

A COMPARISON OF THE TERMINAL ABDOMINAL STRUCTURES OF AN ADULT ALATE FEMALE OF THE PRIMITIVE TERMITE *MASTOTERMES DARWINENSIS* WITH THOSE OF THE ROACH *PERIPLANETA AMERICANA*.*

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Through the kindness of Dr. Tillyard, I was able to describe and figure the terminal abdominal structures of an adult alate male and female *Mastotermes*, as well as the ovipositor of the soldier caste of this intensely interesting termite (Crampton, 1920), but since I was allowed to retain only one alate specimen, I preferred to keep it intact for future study, instead of risking injuring it irreparably in attempting to force apart the plates at the tip of the abdomen to see what might lie beneath them, so that only the external features were figured in the earlier paper on *Mastotermes*. Recently, however, my curiosity got the better of me, and upon forcing down the terminal ventral plate of my specimen (which unfortunately necessitated tearing its basal connection to some extent) I was delighted to find hidden beneath the "hypogynum" (hg of Fig. 2) a fully formed ovipositor composed of three pairs of well-developed valves—a thing never before found in any winged termite, so far as I am aware!

The parts at the base of the ovipositor of the specimen from which the accompanying drawing was made were much shrunk, and since I have not been able to examine a specimen in which the parts are more normal, and since I did not wish to do more damage to my only specimen than was absolutely necessary to expose the ovipositor sufficiently to examine and sketch the parts without dissecting them out, the accompanying figure of the ovipositor of *Mastotermes* is not as accurately detailed as I am hoping to figure the parts of an alate female, when I can obtain more material for dissection and study. The ovipositor of *Mastotermes*, however, is such a unique structure, and this termite is of such great phylogenetic importance, that I have ventured to present the main fea-

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tures of the ovipositor, leaving the more detailed description until material for dissection is available.

The terminal abdominal structures of an adult female roach (Fig. 1) are somewhat more primitive than those of the adult female of *Mastotermes* (Fig. 2), so that it is preferable to define the parts in the roach before taking up the comparison of the parts in the two insects. As has been shown by Wood-Mason, 1879, Walker, 1919-1922, and others, the ovipositor of immature female roaches is much more like that of the primitive Apterygotan *Machilis* in character than is true of the ovipositor of an adult female roach. In the immature roaches, the limbs of the ninth abdominal segment (which form the dorsal and inner valvulae of the ovipositor) consist of the following parts: A short, broad coxite, homologous with the protopodite of a biramous Crustacean pleopod, forms one of the dorsal valves of the ovipositor, and bears at its tip a stylus which represents the exopodite of a Crustacean limb, while the endopodite of the limb is represented by the inner valve of the ovipositor. When the roach becomes adult, the stylus becomes lost, and the coxite which bore it becomes elongated to form the slender dorsal valve, or dorsovalvula *dv* of Fig. 1 (also called the lateral gonapophysis). The inner valve becomes the intervalvula *iv* of Fig. 1 (also called posterior gonapophysis), while the antero-lateral portions of the ninth sternite become somewhat displaced and form the plates termed the valvifers by Crampton, 1917. The ventral valvulae or ventrovalvulae *vv* of Fig. 1 (also called anterior gonapophyses) probably represent the endopodites of the limbs of the eighth abdominal segment. The styli of these limbs are not present in immature roaches. The coxites of the limbs of the eighth abdominal segment are probably represented by the basal plates of the ventral valvulae called the basivalvulae by Crampton, 1917.

As was mentioned above, the ovipositor of the adult female roach (Fig. 1) consists of a pair of dorsal valvulae *dv*, a pair of intermediate valvulae *iv*, and a pair of ventral valvulae *vv*, of which the dorsal and intermediate valvulae belong to the ninth abdominal segment, while the ventral valvulae belong to the eighth abdominal segment. Similarly, in the adult alate female of *Mastotermes*

(Fig. 2) there is a pair of dorsal valvulae *dv*, a pair of intermediate valvulae *iv*, and a pair of ventral valvulae *vv*, which are extremely like those of the roach, and clearly indicate that the Isoptera are very closely related to the Blattids, as is also shown by many other characters such as the nature of the wings of *Mastotermes*, the character of the cervical sclerites, etc.

In the female roach (Fig. 1) there is a modified portion of the eighth abdominal sternite *sg* (called the subgenitale by Crampton, 1917) situated below the genital aperture. A similar structure occurs in the Mantids, but I could not detect any traces of it in my specimen of *Mastotermes* without tearing the parts more than I care to do at this time. The subgenitale *sg* of Fig. 1 becomes the subgenital plate (modified eighth sternite) in Orthoptera, Phasmids, etc.

In the Isoptera, Blattids, and Mantids (*i.e.*, the insects belonging to the superorder Panisoptera) the seventh sternite becomes elongated posteriorly to form a subgenital valve or hypogynum *hg* of Figs. 1 and 2, which partly conceals the ovipositor in Mantids, and completely hides the ovipositor in most Blattids and such termites as have an ovipositor. I do not know what function this structure has in *Mastotermes*, but in the roach shown in Fig. 1 the inner walls of the hypogynum *hg* form the lining of an oothecal cavity in which the ootheca is carried about by the mother roach for a period, and the membranous lining of the distal portion of the hypogynum, in particular, serves to protect the egg capsule until the walls of the ootheca become hardened. It is probable that in Blattids, Mantids, and Isoptera the hypogynum forms a genital cavity functioning in the process of mating. In the roach shown in Fig. 1 the hypogynum is divided into a basal region or basihypogynum *bhg*, and a distal region or distihypogynum *dhg*, the latter being partly divided by a longitudinal cleft into two lobes connected by a portion of the distihypogynal membrane. During the period of carrying the ootheca the distihypogynal membrane becomes distended (as is also true of the general membrane in the region of the ovipositor), and plays an important rôle in protecting the ootheca, as was mentioned above.

The paraprocts *pa*, or parapodial plates of the termite shown in

Fig. 2, are quite like the paraprocts *pa* of the roach shown in Fig. 1; but the cerci *ce* of the termite are not as well developed as those of the roach. Certain termites, such as *Architermopsis*, however, have quite large and well-developed cerci. In this connection, I would call attention to the fact that certain sawflies have long slender cerci quite suggestive of those of *Architermopsis*, as I hope to show in a subsequent paper dealing with the anatomy of the sawflies.

In the Isoptera and Blattids the epiproct *ep* (Figs. 1 and 2) is largely formed by the tenth tergite, and in the Mantids also the tenth tergite is large (and the eleventh tergite becomes greatly reduced and is largely concealed by the tenth). I am not sure that the posterior portion of the plate labeled *ep* in Fig. 1 is not the representative of the eleventh tergite, but I have provisionally interpreted it as a posterior portion of the tenth tergite. The ninth and eighth tergites labeled *8^t* and *9^t* in Fig. 1 are greatly narrowed in the roach there depicted, but in other roaches they are a little broader. In the absence of a marked reduction or narrowing of these tergites in the Isoptera, the latter resemble the Phasmids and Orthoptera in some respects.

Taking the terminal structures in general, *Mastotermes* resembles the Blattids more than any other insects, and in connection with other features such as the venation of the wings, the character of the cervical sclerites, etc., a study of the ovipositor, hypogynum, etc., in *Mastotermes*, would materially strengthen the view that the Isoptera are more closely related to the Blattids than to any other living insects, and likewise indicates that the superorder Panisoptera (composed of the Blattids, Mantids, Isoptera, etc.) is a natural one. In some respects, the Dermaptera bear a marked resemblance to the members of this superorder, but for the present, at least, I would leave the Dermaptera in the superorder Panorthoptera (including the Orthoptera, *s. str.*, the Phasmids, etc.).

The study of the structures present in *Mastotermes* is of prime importance, since it is one of the most primitive representatives of the order Isoptera, and the Isoptera are in many respects the nearest living representatives of the Protorthoptera-like ancestors

of the Psocids (including the Zoraptera) and the Hymenoptera (with their holometabolous allies). In this connection, it should be noted that organisms are not equally primitive or equally specialized in all parts of their bodies (*i.e.*, an individual may be heterarchaic or heterocaenic in different parts of its body) and on this account it is not safe to use one set of features in attempting to determine the ancestry of insects in general. Thus the presence in all known Isoptera of a laterosternite, or lateral plate of the sternal region of the meso- and metathorax (which is found in many immature Ephemerids, Plecoptera, and other primitive insects, as well as in the adults of the Embiids, Dermaptera, Grylloblattids, etc.), while no known Blattid has retained this plate in its primitive condition, would preclude deriving the Isoptera directly from the Blattids as Handlirsch, 1921, has done; and this, together with many other features, clearly indicates that the Isoptera are descended from types ancestral to the Blattids (such as the Protoblattids) or the common Protoblattid-Protorthopterian stock called the Prodictyoptera. In fact, as I have pointed out in a recent paper (Crampton, 1922), the wings of the primitive Isoptera, such as *Mastotermes*, partake of *both* Protoblattid and Protorthopterous characters, and hence the Isoptera were probably descended from the common Protoblattid-Protorthopterian stock (*i.e.*, the Prodictyoptera), from which the Blattids and Mantids were also derived.

In the paper describing the ovipositor of the mature female of the soldier caste of *Mastotermes* (Crampton, 1920) I emphasized the fact that the ovipositor of this *mature* termite resembled the ovipositor of an *immature* female roach in that the styli were present in both, and the coxites of the ninth abdominal segment were short and broad in both. These features are a retention of the primitive condition of the coxites and styli exhibited by such archaic Apterygota as *Machilis*. The ovipositor of an *adult* alate female of *Mastotermes* is like the ovipositor of an *adult* roach, but the ovipositor of an *adult* (or mature) female or worker of *Mastotermes* is like the ovipositor of an *immature* roach, so that the condition occurring in the ovipositor of the mature soldier or worker termite may be regarded as an arrested primitive infantilism (archi-

paedism) carried over into, or retained by, the mature stages of the insect. Why the soldier and worker caste should exhibit this "primitive infantilism" (archipaedism), while the alate adult female does not, is not apparent, unless the worker and soldier castes represent stages more primitive than the alate females do—a conclusion to which few entomologists would subscribe!

The tendency nowadays is to attribute to "convergence" (supposedly the result of the operation of similar environmental conditions) many of the resemblances between the different orders of insects, which, in some cases at least, are really the result of the operation of the same factors inherited from a common source. Despite the protests of Mr. Bryan and the Oklahoma legislature, most scientists, I believe, will attribute the close resemblance between man and the higher apes, for example, to the presence in both of a great number of factors (genes or determinants) inherited from a common source. Man and the lemurs have fewer factors in common, and hence resemble each other more remotely. Man and the rest of the mammals have still fewer factors in common, and hence resemble each still more remotely, and so on, "ad infinitum." The vertebrates all bear a certain fundamental resemblance to each other, due to the retention in all of them of certain factors (genes or determinants) in common, and similarly, the arthropods resemble each other in their fundamental features due to the presence in all of them of certain factors which they all inherited in common. Now, if all arthropods can inherit some factors from a common ancestry, why can not several orders of insects descended from a common source inherit a number of factors (genes or determinants) in common, from their common ancestry, and why is it not reasonable to suppose that the presence of certain factors in common (inherited from a common source) in two or more orders of insects descended from the same ancestral group, will cause the derived orders to parallel each other rather closely in certain of their evolutionary tendencies? I can see no objection to this view, and it appears to me that the closeness of the parallelism in the two orders in question will be in direct proportion to the numbers of factors they have inherited in common. Resemblances resulting from such a "parallelism" due to the in-

heritance of certain factors in common by two groups of animals (*i.e.*, euparallelism or homogenic parallelism) represent true homologies, and are hence to be distinguished from superficial resemblances due to "convergence" or "parallelism" in the usual sense of the word, since the latter resemblances are more of the nature of "analogies." I believe that the tendency to develop social habits exhibited by certain Isoptera, Hymenoptera, Psocids, etc., is a case of euparallelism (or homogenic parallelism) due to the operation of certain factors (genes or what-not) inherited from a common Protorthopteroid ancestry, and I also believe that many cases of resemblance now regarded as the result of "convergence" (*i.e.*, supposedly due to the action of similar environmental conditions) are in reality instances of euparallelism (*i.e.*, are due to the operation of factors inherited in common), but since this idea has been developed in another paper (Crampton, 1922_a), there is no necessity of discussing it further here.

In connection with the preceding discussion of the relationship of the Isoptera to the Orthoptera, the fact that the Grylloblattids are the nearest allies of the Isoptera among the Orthoptera (*s. str.*), and the fact that the Isoptera serve to connect the Orthoptera (including the Grylloblattids) with the rest of the Blattoid insects (*i.e.*, the Panisoptera) in many respects should have been more strongly emphasized. Among the Orthopteroid insects (Panorthoptera) the Phasmids are very closely allied to the Grylloblattids (*i.e.*, in the nature of their head capsule, tarsi, tergal plates, and terminal structures) and the Phasmids are somewhat nearer the Mantids among the Panisoptera than they are to the Isoptera. Thus the Isoptera are not the only important forms among the Blattid-like insects (Panisoptera) which approach the Protorthopterous ancestors of the Orthoptera, but they have retained many features suggestive of these ancestors of the Orthoptera (as well as the ancestors of the Psocids and even the Hymenoptera and their allies), so that a study of the Isoptera is of considerable interest from the standpoint of phylogeny, and more attention should be given them in this respect than has hitherto been accorded them.

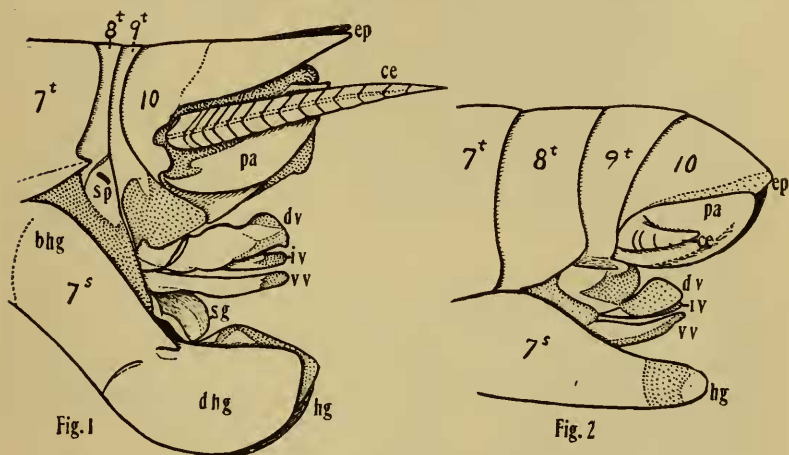
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ABBREVIATIONS.

- 7^t, 8^t, 9^t, etc. . . Tergites of the seventh, eighth, and ninth abdominal segments.
- 7^s Sternite of the seventh abdominal segment.
- bhg Basal region of hypogynum (basihypogynum).
- ce Cercus.
- dhg Distal region of hypogynum (distihypogynum).
- dv Dorsal valves of ovipositor (dorsovalvulae), also called lateral gonapophyses.
- ep Epiproct or pygidium.
- hg Seventh sternite prolonged beneath ovipositor (hypogynum).

- iv*.....Intermediate valves of ovipositor (intervalvulae), also called posterior gonapophyses.
pa.....Paraprocts or parapodial plates.
sg.....Eighth sternite or subgenitale, which forms subgenital plate in Orthoptera.
sp.....Spiracle.
vv.....Ventral valves of ovipositor (ventrovalvulae), also called anterior gonapophyses.



EXPLANATION OF PLATE.

FIG. 1. Lateral view of terminal abdominal segments of the roach *Periplaneta americana*.

FIG. 2. Same of the termite *Mastotermes darwiniensis*.

A Correction.—The record of *Amblyscirtes vialis* Edwards in my list of butterflies collected in Florida, March, 1921, BULLETIN xviii, 1, page 27, is incorrect; please substitute in place of same *Amblyscirtes alternata* Grote and Robinson. In nomenclature this follows Dr. Lindsey in his "*Hesperioidea of America North of Mexico*," and not Barnes and McDunnough's *Check List*.—E. L. BELL, Flushing, L. I., N. Y.